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Neural Representation of Articulable and Inarticulable Novel Sound Contrasts: The Role of the
Dorsal Stream

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APPROVAL PAGE

Master of Science Thesis

Neural Representation of Articulable and Inarticulable Novel Sound Contrasts: The Role of the Dorsal Stream

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Abstract

The extent to which articulatory information embedded in incoming speech contributes to the formation of new perceptual categories for speech sounds has been a matter of discourse for decades. It has been theorized that the acquisition of new speech sound categories requires a network of sensory and speech motor cortical areas (the “dorsal stream”) to successfully integrate auditory and articulatory information. However, it is possible that these brain regions are not sensitive specifically to articulatory information, but instead are sensitive to the abstract phonological categories being learned. We tested this hypothesis by training participants over the course of several days on an articutable non-native speech contrast and acoustically-matched inarticulable non-speech analogues. After reaching comparable levels of familiarity with the two sets of stimuli, activation was measured in fMRI as participants passively listened to both sound types. Results from multivariate decoding of neural responses indicated that activation patterns in left IFG, MTG, and SMA provided better information for decoding articutable sounds compared to the inarticulable sounds, consistent with the proposed role of the dorsal stream during phonetic learning. Curiously, decoding of category membership for the articutable speech contrast alone revealed a series of left and right hemisphere regions *outside* of the dorsal stream that have previously been implicated in the emergence of non-native speech sound categories.

Keywords:

Speech perception, fMRI, MVPA, speech articulation

Introduction

Whether an infant learning her first language, or an adult learning his fifth language, in language acquisition the learner must learn to perceive as well as produce new speech sounds. In typical language acquisition, these two processes (perceptual and articulatory learning) develop in tandem, although not necessarily on the same timeline (Tsao, Liu & Kuhl, 2004). However, in laboratory conditions, we know that individuals can learn to distinguish complex auditory speech and non-speech categories without learning to produce these same categories. At issue is the degree to which articulatory information associated with speech is recruited even in the absence of articulatory learning. That is, when one learns a new phonetic category without learning to produce the same category, are speech motor representations recruited?

Models of speech perception like the motor theory of speech (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967) and subsequent direct realist approaches (Best, 1995; Fowler, 1986), make explicit predictions about the formative role of articulatory codes in speech perception. In these models, motor or articulatory representations are the objects of perception, and must be acquired and then accessed to achieve robust comprehension (see Gallantucci, Fowler, & Turvey, 2006 for a review). Thus, learning to discriminate between a pair of speech sounds like /b/ and /d/ (which are similar acoustically) requires that the listener access information the articulatory gestures used to produce those sounds.

Though not explicitly linked, the dual stream model of speech processing (Hickok & Poeppel, 2007) makes biological predictions that also implicate motor systems not in speech sound *perception*, but speech sound *learning*. Specifically, the dorsal stream pathway (consisting of brain regions like the inferior frontal gyrus (IFG), pre-motor cortex (PMC), and temporal-parietal junction (TPJ)) is claimed to play critical role in auditory-motor integration and serves as a “neural mechanism that both codes and maintains instances of speech sounds,” which can then be later used to aid in production as well as in perception (p. 399). According to this view, during learning of new speech sounds, listeners code the incoming articulatory gestures in dorsal stream areas in preparation for future speech output (Hickok & Buchsbaum, 2003). Notably, once speech sound representations have been learned, dorsal stream activation is no longer thought to be required during perception-only tasks.

The role of the dorsal stream during speech perception (for established speech categories and newly learned ones) has been a matter of significant debate, as has the role of articulatory codes during speech perception in general (see, for instance, Lotto, Hickok, & Holt, 2009, Wilson, 2009, Scott, McGettigan, & Eisner, 2009). If articulatory codes are accessed as a matter of course during perception of speech categories, it should follow that the encompassed brain regions are sensitive to differences in articulation between speech sounds during speech perception, especially during speech sound learning (see Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007; Wilson & Iacoboni, 2006; Wilson, Saygin, Sereno, & Iacoboni, 2004). While evidence for sensitivity to place/manner of articulation differences is apparent in left superior temporal gyrus using electrocorticography (Mesgarani, Cheung, Johnson, & Chang, 2014), it is less clear that *dorsal* stream speech motor regions are involved in perception of established, mature speech categories. Using a univariate fMRI approach, Pulvermüller et al. (2006) found differential activation in lip- and tongue-dedicated regions of precentral gyrus in response to the syllables /p/ and /t/, which differ in place of articulation. These results were supported by findings from Correia, Jansma, and Bonte (2015), who used a multivoxel pattern analysis (MVPA) to identify brain regions that could classify neural responses to stimuli based on specific articulatory features independent of phonemic category (and subsequent acoustic variation). Activation patterns in pre-motor and motor areas (among other regions) could distinguish place and manner of articulation contrasts, even though the classifier was trained on responses to one phonological category (stop consonants) and tested on responses to another (fricatives). However, both Arsenault and Buchsbaum (2015) and Arsenault and Buchsbaum (2016) failed to find any dorsal stream regions that were sensitive to different articulatory dimensions of passively heard syllables in both univariate (attempting to replicate Pulvermüller et al.'s results) and multivariate analyses, calling into question the sensitivity of the dorsal stream to learned phonological contrasts.

As noted above, there is contradictory evidence that dorsal stream regions are sensitive to articulatory contrasts during speech perception. However, even in the studies that support the activation of the dorsal stream during speech processing, an alternative explanation exists: It is possible that what is being observed is IFG sensitivity to abstract categories at large, and not specifically the articulatory differences between sounds. That is, during speech perception,

inferior frontal structures may not be coding articulatory differences between sounds (like the difference in lip protrusion in the production of /i/ and /y/), but instead is coding the ultimate product of those gestures, which are two distinct phonetic categories. IFG sensitivity to speech categories has been established in a number of studies (Hutchison, Blumstein, Myers, 2008; Lee, Turkeltaub, Granger, & Raizada, 2012; Myers, 2007; Myers, Blumstein, Walsh, & Eliassen, 2009), but these studies do not disentangle the issue of articulatory codes versus abstract categories as the two are fundamentally confounded in established speech categories. In each of these previous studies, participants were presented with isolated speech sounds in their native language. These well-established perceptual categories may activate articulatory representations of the same sound by association rather than as a means to perceive the sound itself. That is, upon hearing “da”, one may automatically activate gestural codes for producing “da”, whether or not this articulatory information is necessary for retrieving the speech sound category. Further, as argued in the dual stream model, the dorsal stream may only be recruited during learning, when participants are learning the links between auditory and motor representations of sounds. Thus, to fully test the predictions of this model, it is necessary to present listeners with a situation in which a new speech category is acquired alongside an acoustically matched, inarticulable contrast in order to fully establish what dorsal stream activation may actually reflect.

Liebenthal, Binder, Spitzer, Possing, and Medler (2005) and Liebenthal et al. (2010) explored this idea by contrasting brain activation from familiar speech sounds (a continuum from /b/ to /d/) with that of an acoustically unfamiliar matched non-speech continuum (created by spectrally inverting the first formant of the speech continuum). Although when subjects have minimal exposure to the speech and non-speech continua (Liebenthal, et al., 2005), no dorsal stream differences emerged, once subjects were trained on the same stimuli for four days, (Liebenthal et al., 2010), some dorsal stream recruitment is seen. That dorsal stream recruitment arises only during the learning process is consistent with the dual stream model, but paradoxically, dorsal stream engagement is not preferentially seen for speech (articulable) stimuli. Instead, several significant clusters in left IFG, bilateral postcentral gyrus, and bilateral supplementary motor area display greater activation at post-test for the *non-speech* continuum that could not be articulated by a human vocal tract. In a conjunction analysis, in which the neural changes as a result of training were compared across the speech and non-speech continua,

left IFG was identified as sensitive specifically to learning in the non-speech continuum. This provides further evidence that during learning, IFG activation more likely reflects the emergent category status of the non-speech stimuli as listeners begin to form perceptual categories rather than a reflection of articulatory codes (Myers, et al., 2009).

Desai, Liebenthal, Waldron, and Binder (2008), used a similar paradigm to Liebenthal et al. (2005), but critically substituted sine-wave speech versions of both the speech (/b/-/d/) and non-speech continua (spectrally rotated /b/-/d/). Adopting the labels from this study, we will refer to them hereafter as “phonemic” and “non-phonemic,” respectively, to differentiate from the natural speech versions of these stimuli in previous studies. Sine-wave speech is created by taking the spectral center and power of each of the formants in a speech sound, and then creating a sine-wave tone at the same frequency and power (Remez, Rubin, Pisoni, & Carrell, 1981). The resulting sound contains approximately the same *distinctive* spectral information as the original speech sound, but is not perceived as speech or speech-like until the listener is informed of the intended message, after which listeners often report being able to understand the message. These stimuli allowed the authors to control for familiarity and to manipulate the availability of articulatory information by revealing to participants midway through the experiment that one of the continua (the “phonemic” continuum) was made from familiar speech sounds. Dorsal stream recruitment was observed at post-test, where greater activation in left inferior frontal gyrus and left precentral gyrus was seen for the “phonemic” continuum compared to the “non-phonemic” continuum. It seems possible that after being informed the “phonemic” continuum was supposed to reflect two familiar speech sound categories, listeners began to recover some of the articulatory code used to create those sounds, and as a result the dorsal stream was recruited during learning. But again, this possibility does not exclude that neural activation reflects the emergence of two distinct categories, as perception of the “phonemic” continuum shifted from a continuous mode to a categorical mode during post-test.

To investigate the role of the dorsal stream during the learning of new speech sounds, we attempted to equate the degree of familiarity between the two stimulus sets being learned, as well as manipulate articulatory feasibility. While both of these have been manipulated independently, to our knowledge no study has controlled for both of these variables simultaneously. We take a

similar approach to Liebenthal et al. (2005, 2010) by introducing a set of articlable (non-native speech) vs. inarticlable (impoverished sine-wave speech) sounds. Like Desai et al. (2008), we used sounds that didn't initially have established categories for our listeners, therefore requiring participants to learn both sets of sounds (unlike Liebenthal et al., 2005, 2010). However, in Desai et al., articulatory information is only indirectly implied in their phonemic continuum, as it is sine-wave speech. There is no guarantee that participants are activating articulatory representations of the source stimuli, and their results could reflect listeners treating the sine-wave speech as inarticlable sounds but with a defined category structure. Therefore, we chose to use a non-native speech sound contrast to ensure that articulatory information is theoretically available, but the contrast is still as unfamiliar as the impoverished sine-wave speech contrast. Listeners are then trained to the same accuracy on both contrasts, after which two competing hypotheses can be investigated. First, following the logic of the dual stream model of speech perception, dorsal stream regions should only be recruited for auditory-motor integration during the learning of articlable sounds. Alternatively, dorsal stream regions (especially IFG) may play a more general role in categorical decisions and will be equally recruited during learning of both articlable and inarticlable sounds (so long as the two sounds are equally well learned).

The question at hand is especially suited to the use of multivoxel pattern analysis (MVPA, Haxby et al., 2001) because these techniques can provide a clue as to the nature of the information stored in different areas of cortex. If patterns of activation are distinctive enough to classify stimulus types, it implies that there is systematic neural representation for some property of that stimulus. Further, the differences in activation in response to a contrast like /b/ and /t/ may not be in separate areas of cortex, but better characterized by a distributed pattern of activation (including non-adjacent voxels), the kind of informational code that MVPA is sensitive to. By using signal decoding techniques, we ask not only whether articulatory vs. auditory regions are recruited, but whether the information content of those regions distinguishes between the two categories in each contrast.

We attempted to answer this question by using a multi-day training study in which participants were trained to equal degrees of familiarity on an unfamiliar (but articlable) non-native phonetic contrast (the /i/ vs. /y/ contrast found in languages like French), as well as acoustically-

matched impoverished sine-wave analogues of the same contrast. After three days of training, participants then engaged in a passive fMRI task in which they heard tokens from the two continua they were trained on. A series of univariate and multivariate analyses were performed on the fMRI data to determine the neural architecture involved in learning of new sounds, and how the articulatory feasibility of that sound impacts that architecture.

Materials and method

1.1 Participants

34 students were recruited from the XXX University. All participants indicated that they were right-handed, monolingual English speakers with normal hearing and no history of neurological or language disorders. Eight participants were excluded (failure to complete all four sessions, $n = 5$, incomplete MRI data, $n = 2$, withdrawal, $n = 1$), leaving data from 26 participants (ages = 18-22 years, females = 16, males = 10) for analysis. Written informed consent was obtained from every participant in accordance with the guidelines of the XXX ethics committee. Participants were paid for their participation.

1.2 Stimuli

1.2.1 Speech stimuli

The speech stimuli consisted of tokens taken from a seven-step vowel continuum from /i/ (front unrounded vowel, found in English in words like “leaf”) to /y/ (front rounded vowel found in languages such as French). This contrast was chosen because /y/ is not found in American English phonology and monolingual English speakers consistently struggle to discriminate these vowels without training (Levy & Strange, 2008; Darcy et al., 2012).

Natural speech tokens of /y/ and /i/ were produced by a male native speaker of Parisian French, and the /y/ token was then transformed into synthesized speech using the “to KlattGrid” function in PRAAT (Boersma, Paul, & Weenink, 2017) to allow for precise control over acoustic properties. F1, F2, and F4 were fixed at the average values derived from the natural /y/ production, and F3 was systematically lowered in 7 equal Bark scale steps until the F3 value was equivalent to the naturally produced /i/ token’s F3 value, creating a continuum from /y/ to /i/. F5 was removed as it is uninformative to the contrast of interest. The synthesized /i/ and /y/

endpoints were submitted for pilot testing to five native speakers of French, who accurately identified the intended vowels and deemed them natural sounding. All tokens had a duration of 432 ms and were scaled to an intensity of 84 dB. Stimuli were delivered over headphones at a volume adjusted by the participant to a loud yet comfortable listening level.

1.2.2 Sine-wave stimuli

Non-speech acoustic analogues of the speech stimuli were created by transforming the vowel continuum described in the previous section into sine-wave speech. This was achieved using a PRAAT script created by Chris Darwin (available at http://www.lifesci.sussex.ac.uk/home/Chris_Darwin/Praatscripts/SA). The resulting seven tokens were then stripped of the sine-wave equivalents of F1 and F4, leaving only the critical F2-F3 contrast in place to reduce the likelihood that they would be perceived as speech-like (see Figure 1). The resultant two-formant sine sweeps are thus acoustically matched to the diagnostic information in the vowel continuum (the frequency of F3), but critically during initial pilot testing ($N = 11$) were never indicated to be perceived as speech (participants frequently described them as “chirps”, “bird sounds”, or “robot sounds”). The same pilot testing also revealed that a single session was sufficient for participants to reach near ceiling accuracy in categorizing sine-wave analogue tokens using the explicit perceptual fading training task described in the following sections ($M = 97.7\%$, $SD = 15\%$). All tokens had a duration of 432 ms and were scaled to an intensity of 80 dB.

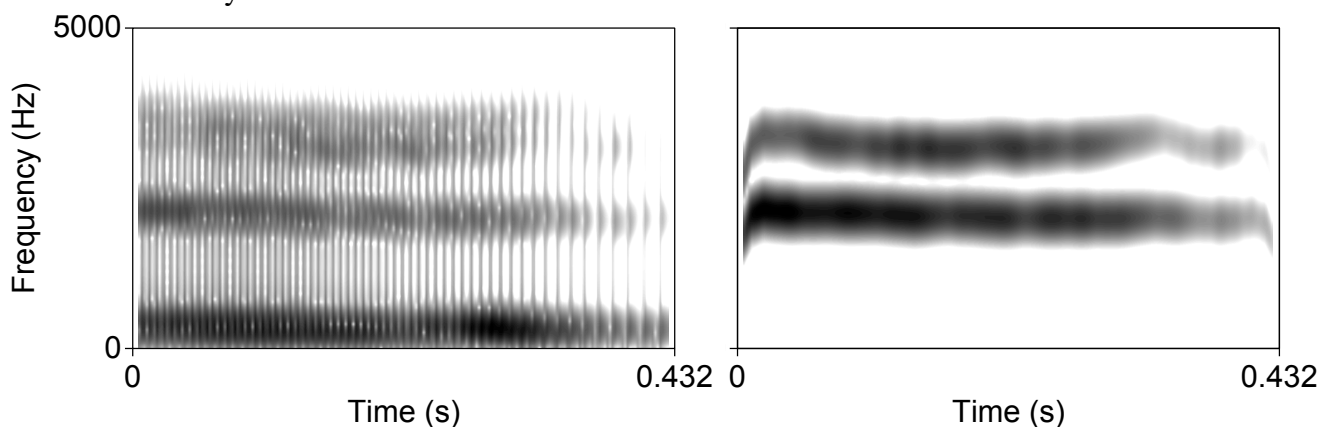


Figure 1. Spectrograms of the first step of the vowel (left) and sine-wave (right) continua.

1.3 Experiment schedule

The study took place over four consecutive days (see Figure 2); on the first day, participants went through the informed consent process and completed the training paradigm for the vowel tokens. On the second day, participants returned and repeated training for the vowel tokens. On the third day, participants again repeated the vowel training followed by the sine-wave training paradigm. Finally, on the fourth day participants completed a short refresher on both stimulus sets, in which participants were refamiliarized with the correspondence between continuum sounds and the category they map on to, and then completed the fMRI task. The discrepancy in the number of training sessions between the vowel stimuli and the sine-wave stimuli was a result of earlier pilot testing, which indicated that it took participants one session to reach a threshold of at least 80% accuracy in the most difficult training block on the sine-wave stimuli, but three days to reach the same criteria for the vowel stimuli. The fMRI task was completed on a fourth day to allow for consolidation of the recently learned sine-wave stimuli, as sleep consolidation has been shown to impact non-native phonetic learning (Earle & Myers, 2015).

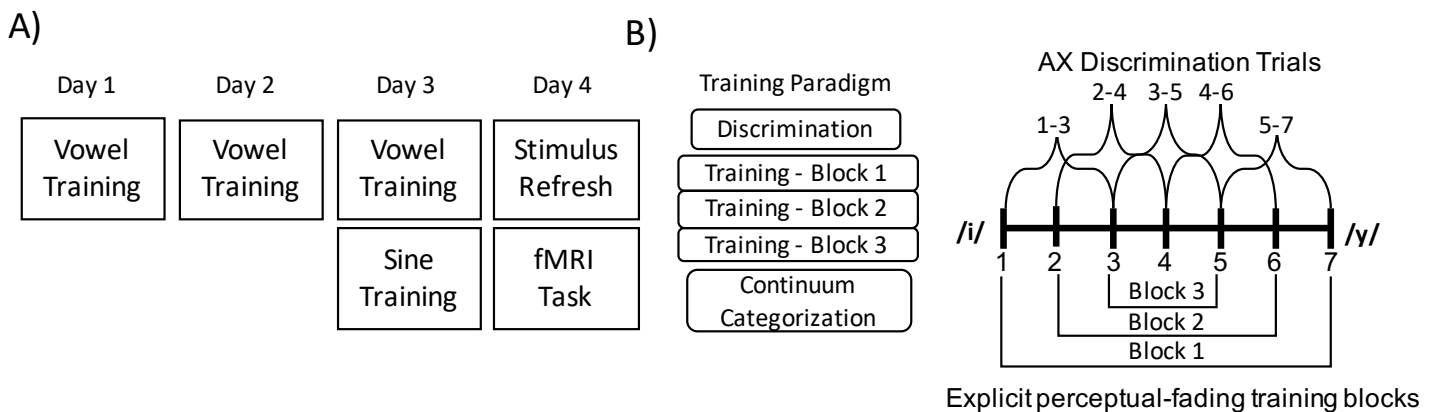


Figure 2. A) Schedule of tasks completed over the course of the four days of training. B) Schedule of the subtasks that comprised both the vowel and sine-wave training sessions. C) Overview of the stimulus pairs used in the discrimination (above the horizontal continuum line) and explicit perceptual fading training (below the horizontal continuum line).

1.3 Behavioral training regimen

The behavioral training paradigm consisted of three subtasks that were identical in structure across both Vowel and Sine training. OpenSesame 3.2.4 (Mathôt, Schreij, & Theeuwes, 2012) was used for stimulus presentation, and all responses were made via a Cedrus RB-840 response box. Participants wore Sony MDR-7506 headphones and were allowed to adjust volume to their most comfortable listening level. All response options were counterbalanced across participants.

1.3.1 Discrimination

At both the beginning and end of the behavioral training paradigm, participants completed an identical AX discrimination task in which they were presented with a pair of tokens from the appropriate stimulus set that were either identical (e.g., step 1 vs. step 1) or two steps apart on the continuum (e.g., steps 1 vs. step 3; steps 4 vs. step 6) and asked to indicate as quickly and accurately as possible if the two sounds were the same or different. All pairs were presented both “forwards” (e.g. step 1 followed by step 3) or “backwards” (e.g., step 3 followed by step 1), with an inter-trial interval of 500 ms. There were seven pair types where the two tokens presented were identical and ten pair types where the stimuli differed. Each pair was presented 11 times, for a total of 187 trials. Accuracy of response and reaction time (RT) were both recorded as outcomes of interest, and d' , an unbiased measure of sensitivity, was calculated from participant’s responses. Trials in which participants failed to respond before the trial timed out (6000 ms) were considered an incorrect response.

1.3.2 Perceptual fading training

Explicit training on the sound categories used a perceptual fading paradigm where participants were asked to map the two halves of the continuum to a different colored square. On each successive block, the acoustic difference between the two tokens that participants were asked to identify was reduced. To familiarize participants with the two categories they would be hearing, they were first shown a colored square and played 10 repetitions of the continuum endpoint token that would thereon be arbitrarily associated with that colored square (e.g., a red square would appear on the screen and the /i/ endpoint token would play).

DORSAL STREAM DECODING OF ARTICULABLE AND INARTICULABLE SOUNDS

In the first training block (labeled as “easy”), participants were asked to identify as quickly and accurately as possible which colored square corresponded to step 1 and step 7. On the second training block (labeled as “medium”), participants were asked to identify which colored square corresponded to continuum step 2 and continuum step 6. On the third training block (labeled as “hard”), participants were asked to identify which colored square corresponded to continuum step 3 and continuum step 5, the tokens which lay on opposing sides of the acoustic boundary. Notice that step 4, the midpoint of the continuum, was not presented during training.

Each block consisted of 60 trials (30 repetitions of each token), and participants were required to achieve an 80% accuracy threshold in order to ascend to the next block. If participants did not reach threshold by the end of the block, they would repeat that same block up to three times before being forced to move on to the subsequent block. Therefore, a given participant could experience between one and three repetitions of each block, depending on how quickly they advanced to more difficult blocks. Participants received explicit feedback during the task. Accuracy of response and RT were both recorded as outcomes of interest.

1.3.3 Continuum categorization

Following training, participants engaged in a two-alternative forced choice task in which they were asked to identify the colored square that corresponded to the sound being presented, with no feedback. There were 10 randomly-presented repetitions of each token from the full seven-step continuum, for a total of 70 trials. The proportion of step 7 responses (which corresponded to the /y/_{Vowel} and /y/_{Sine} endpoints in the Vowel and Sine conditions respectively) per continuum step were then calculated. Trials in which participants failed to respond were omitted from analysis.

1.4 Imaging methods

1.4.1 fMRI design and procedure

Before entering the scanner, participants completed a brief task in which they were refamiliarized with the stimuli that would be presented during the fMRI task. Participants were first presented with a colored square while five repetitions of each of two tokens from that category were played. Following this, participants engaged in a two-alternative forced choice

(2AFC) task in which they were asked to identify which colored square corresponded to the sound presented. Each of the four tokens were repeated 30 times each, and this was repeated for both the Vowel tokens and the Sine tokens, leading to a total of 240 trials for the 2AFC task. Explicit feedback was provided during this task.

Participants were instructed to listen attentively, and told that on some trials a stimulus would be presented more quietly than normal. When this happened, they should press any button on the MRI-safe response devices held in both hands. These catch stimuli consisted of a randomly chosen token from the eight Vowel and Sine tokens presented at 20 dB lower intensity. Participants completed a brief training during the structural scan acquisition to familiarize them with this task. Imaging data from catch trials were modeled in participant level analyses but did not contribute to group-level analyses. Participants were on average quite accurate at detecting catch trials ($M = 90\%$, $SD = 30\%$). Stimuli were delivered by OpenSesame 3.2.4. The volume was set to a comfortable listening level as determined by each participant.

The fMRI experimental paradigm consisted of ten runs, with run order randomized between participants. Trials within each run were presented in a fixed, pseudorandom order determined using the OptSeq2 tool (<https://surfer.nmr.mgh.harvard.edu/optseq/>). Steps 1, 3, 5, and 7 from both the Vowel and Sine continua were each repeated 15 times per run, along with 15 stimuli used for the catch task described in the previous paragraph, resulting in 150 presentations of each stimulus over the course of the experiment. An auditory stimulus appeared in all but 25 of the silent gaps during scanning, for an average inter-trial interval of 2390 ms. Each run consisted of 161 volumes.

1.4.2 Acquisition parameters

Anatomical and functional MRI data were collected with a 3-T Siemens Prisma scanner (Erlangen, Germany). High resolution 3-D T1-weighted anatomical images were acquired using a multiecho magnetization prepared rapid gradient echo sequence (MPRAGE: repetition time [TR] = 2400 ms, echo time = 2.22 ms, inversion time = 1000 ms, 0.8-mm³ isotropic voxels, 320 × 320 matrix) and reconstructed into 208 slices. Functional EPIs were acquired using an accelerated multiband sequence in ascending, interleaved order (52 slices, 2.5-mm thick, 2-mm²

axial in-plane resolution, 110×110 matrix, 220-mm³ field of view, flip angle = 62°) and followed a fast, sparse sampling design: Each functional volume was acquired with a 1000 ms acquisition time, followed by 1000 ms of silence during which auditory stimuli were presented (effective TR = 2000 ms). Stimuli were always presented during the silent gap.

1.4.3 Univariate fMRI analyses

Data were analyzed using AFNI (Cox, 1996). Preprocessing for the univariate analyses consisted of first transforming images from oblique to cardinal orientation, followed by motion correction using a six-parameter rigid body transform aligned with each participant's anatomical data set, normalization to Talairach space (Talairach & Tournoux, 1988), and spatial smoothing with a 4-mm Gaussian kernel. Masks were created using each participant's anatomical data to eliminate voxels located outside the brain. Individual masks were used to generate a group mask. Motion and signal fluctuation outliers were removed following standard procedures.

We generated time series vectors for each of the eight continua tokens (Vowel step 1, Vowel step 3, Vowel step 5, Vowel step 7, Sine step 1, Sine step 3, Sine step 5, Sine step 7) as well as the catch trials and any false alarm trials for each participant in each run. These vectors contained the onset time of each stimulus and were convolved with a stereotypic gamma hemodynamic function. The ten condition vectors along with six additional nuisance movement parameters were submitted to a regression analysis. This analysis generated by-voxel fit coefficients for each condition for each participant.

For group level analysis, beta coefficients were submitted to an 2x3 ANOVA in AFNI (using *3dANOVA3*). In the ANOVA, main effects of sound type (Vowel vs. Sine), continuum step (1 vs. 3 vs. 5 vs. 7), and their interaction were estimated.

1.4.4 Multivariate fMRI analyses

Data were preprocessed again using AFNI with a modified pipeline compared to the univariate analyses. Specifically, multivariate preprocessing consisted of first transforming images from oblique to cardinal orientation, followed by motion correction using a six-parameter rigid body transform aligned with each participant's anatomical data set. No blurring or spatial

normalization were performed until after the subject-level analysis to preserve fine-grained spatial information. The same ten condition vectors from the univariate analyses along with six additional nuisance movement parameters were submitted to an individually-modulated regression analysis (using the “stim_times_IM” flag in AFNI’s *3dDeconvolve*), in which each trial for a condition is given its own amplitude estimation, yielding trial-wise beta coefficients (as opposed to run-wise beta coefficients, see Rissman, Gazzaley, & D’Esposito, 2004). The matrices from the output of the individually-modulated regression were then submitted to a least-squares-sum estimation using AFNI’s *3dLSS*, in accordance with best-practices for performing multivariate analyses on fast event-related fMRI designs (Mumford, Turner, Ashby, & Poldrack, 2012; Mumford, Davis, & Poldrack, 2014).

The beta coefficient output from *3dLSS* was then used in a multi-voxel pattern analysis (MVPA) performed in MATLAB using The Decoding Toolbox (TDT, Hebart, Gorgen, & Haynes, 2015). A linear support vector machine (SVM) classification was used with 3 voxel (6 mm) radius searchlight and a leave-one-run-out cross validation scheme, in which the SVM was trained on data from nine runs and tested on a tenth, held out run. The regularization parameter for the SVM was set at $C = 1$. In a searchlight analysis, a roving sphere moves across the whole brain, and in each searchlight sphere an SVM was trained and tested (Kriegeskorte, Goebel, & Bandettini, 2006). The classification accuracy score was assigned to the central voxel of each searchlight. This yielded a subject-level classification accuracy map for each participant in their brain’s native space. The following classifications were performed: /i/ vs. /y/ for vowel tokens (defined as step 1 and step 3 vs. step 5 and step 7, hereafter “/i/_{Vowel} vs. /y/_{Vowel}”), and the analogous sine version (which we will hereafter refer to as “/i/_{Sine} vs. /y/_{Sine}”).

In preparation for group-level analyses, subject-level classification maps were then normalized to Talairach space and blurred with a 4-mm Gaussian kernel. Following this, single-sample t-tests against chance levels were performed for the /i/_{Vowel} vs. /y/_{Vowel} and /i/_{Sine} vs. /y/_{Sine} (using *3dttest++*): t-test output was masked by a group mask which only included voxels present in all 26 participants. In addition, a paired-samples t-test was performed comparing the /i/_{Vowel} vs. /y/_{Vowel} and /i/_{Sine} vs. /y/_{Sine} decodings.

Cluster level correction for multiple comparisons was determined by running 10,000 iterations of Monte Carlo simulations (*3dClustSim*, AFNI) on the group mask. Specifically, we used -acf option in *3dFWHMx* and *3dClustSim* (AFNI) to estimate the spatial smoothness and generate voxelwise and clusterwise inferences. Data were corrected at a cluster level correction of $p < 0.05$ (voxel level threshold of $p < 0.025$, 149 contiguous voxels).

Results

1.5 Behavioral Data Analysis and Results

1.5.1 Vowel Training Results

Perceptual fading training

On average, accuracy during training improved over the course of the three days (see Table 1, Figure 3A). Given the adaptive nature of the paradigm, participants completed varying repetitions of each level of difficulty (“easy”: $M = 1.29$ blocks, $SD = 0.58$; “medium”: $M = 1.28$ blocks, $SD = 0.58$; “hard”: $M = 2.12$ blocks, $SD = 0.90$), and as expected there was a strong negative correlation between the number of blocks completed and average accuracy on the explicit perceptual fading training ($r(24) = -0.92, p < 0.0001$).

Accuracy data during training was submitted to a generalized linear mixed-effects model using the R packages *afex* and *lme4* (Bates, Maechler, Bolker, & Walker, 2015; Singmann, Bolker, Westfall, & Aust 2018). Model selection was achieved by first creating and running all possible permutations of random effects structures, after which a backwards stepping selection procedure was applied to the models that converged (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017). Output from the ANOVA table generated by the *afex* command ‘mixed’ (ran on the appropriate model selected from the earlier described procedure) are reported for all mixed-effects model analyses in this study.

Table 1. *Accuracy during explicit perceptual fading training.*

Training	Easy (1-7)	Medium (2-6)	Hard (3-5)
Day 1 - Vowel	$M = 87.7\%$ ($SD = 33\%$)	$M = 89\%$ ($SD = 31\%$)	$M = 73.9\%$ ($SD = 43.9\%$)
Day 2 - Vowel	$M = 96.2\%$ ($SD = 19\%$)	$M = 93.1\%$ ($SD = 25.3\%$)	$M = 76.9\%$ ($SD = 42.2\%$)
Day 3 - Vowel	$M = 95.7\%$ ($SD = 20.3\%$)	$M = 93.3\%$ ($SD = 25\%$)	$M = 79.4\%$ ($SD = 40.5\%$)
Day 3 - Sine	$M = 93.7\%$ ($SD = 24.3\%$)	$M = 94.9\%$ ($SD = 22.1\%$)	$M = 83.9\%$ ($SD = 36.7\%$)
Means (M) and standard deviations (SD) displayed.			

To examine the degree to which participant's accuracy during vowel training increased over time, a generalized linear mixed-effects model was performed. The selected model included fixed effects for training difficulty level, training day and the interaction of training day and level, as well as by-subject random slopes and intercepts for the interaction between training difficulty level and training day. The model revealed a significant main effect of training difficulty ($\chi^2 = 89.27, p < 0.0001$) and a main effect of training day ($\chi^2 = 7.45, p = 0.02$), with higher accuracy on “easier” blocks consisting of larger intervals on the continuum and higher accuracy on successive days of training, and. The interaction between training difficulty and training day did not reach significance ($p = 0.62$).

Vowel continuum categorization

In general, participants were successful at identifying the endpoints of the continuum, with at least 90% accuracy on average across each of the three training days (see Figure 3B). Responses from the categorization post-test were transformed into a binary outcome variable and then submitted to a generalized linear mixed-effects model with a logit link function (also instantiated in the R package ‘afex’) to assess how categorization of the full continuum changed over the course of the three training days. *P* values were estimated using a likelihood-ratio test. The model selected included fixed effects for continuum step (centered) and training day, with by-subject random slopes and intercepts for continuum step, training day, and their interaction. Output from the model indicated a main effect of continuum step ($\chi^2 = 44.15, p < 0.0001$) and a

main effect of training day ($\chi^2 = 6.08, p = 0.05$), indicating that participants' $/y/_{\text{Vowel}}$ responses increased as a result of the F3 manipulation across the continuum as expected, and that participants' overall proportion of $/y/_{\text{Vowel}}$ responses decreased with more experience with the continuum. The interaction was not significant ($p = 0.82$), indicating no significant change in the steepness of the categorization function over the three days of training.

AX discrimination task

Discrimination data was first separated into pre-test (the first discrimination task completed during that day's training) and post-test (the final discrimination task following that day's continuum categorization task), and "different" trials were collapsed such that discrimination tokens "step 1 – step 3" was considered the same as "step 3 – step 1". Following this, d' was calculated for each of the resulting five "different" tokens for each subject and training day. For the purposes of analysis, the token "3-5" was considered to be between-category (as step 4 of the continuum represents the most ambiguous token in terms of acoustics), and all other tokens were considered "within-category" (Figure 3C).

A linear-mixed effects model was then performed on participant's d' scores, with fixed effects of token type ("between-category" vs. "within-category"), training day, block (pre-test vs. post-test) and their interactions, and by-subject random intercepts. A main effect of token type was found ($\chi^2 = 58.64, p < 0.001$), in that d' scores were higher for the "between-category" token (step 3 – step 5) than the "within-category" tokens. In addition, a main effect of training day ($\chi^2 = 4.13, p = 0.02$) arose indicating that d' scores increased over the course of the experiment. Finally, a main effect of block ($\chi^2 = 4.09, p = 0.04$) was found, indicating overall higher d' scores for post-test compared to pre-test. All interactions were non-significant.¹

¹ Using the acoustic boundary to determine the "between-category" discrimination token ignores the fact that participant's perceptual boundary did not necessarily correspond to acoustic boundary of the continuum. To remedy this concern, we estimated subject-specific perceptual boundaries and fit a linear-mixed effects model using the subject-specific determinations of the "between-category" and "within-category" tokens. Model output did not differ from the analysis using the acoustic boundary. See Figure 3D.

DORSAL STREAM DECODING OF ARTICULABLE AND INARTICULABLE SOUNDS

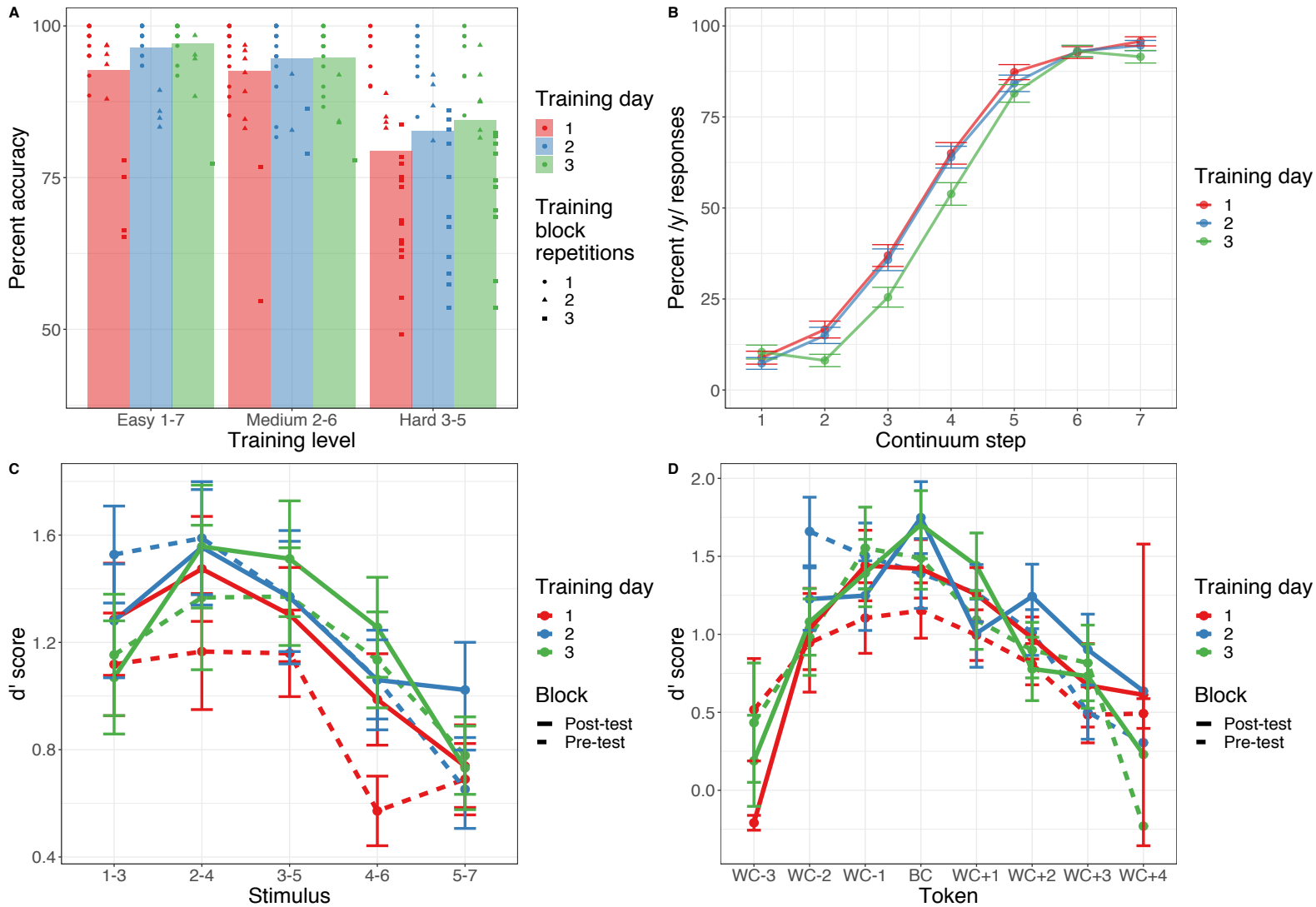


Figure 3. Behavioral data from the vowel training paradigm. A) Accuracy on the explicit perceptual fading training task for the vowel stimuli as a function of training level difficulty. Each point indicates an individual subject's performance, and the shape of the point indicates the number of times that participant repeated that block. B) Responses to the continuum categorization task as a function of $/i/_{\text{vowel}}-/y/_{\text{vowel}}$ continuum step and training day. Error bars indicate standard error. C) d' scores from the AX discrimination task for the vowel stimuli across each stimulus as a function of pre-test and post-test as well as training day. Error bars indicate standard error. D) d' scores from the AX discrimination task for vowel stimuli with respect to the subject-specific determination of the “between-category” (BC) token as a function of pre-test and post-test as well as training day. Error bars indicate standard error.

1.5.1.2 Sine Training Results

Explicit perceptual fading training

Participants again completed varying repetitions of each level of difficulty (“easy”: $M = 1.27$ blocks, $SD = 0.60$; “medium”: $M = 1.35$ blocks, $SD = 0.56$; “hard”: $M = 1.69$ blocks, $SD = 0.84$), and there was a similarly strong negative correlation between the number of blocks completed and average accuracy on the explicit perceptual fading training ($r(7) = -.86, p = 0.003$).

To examine the efficacy of the single training session on identification of the two Sine tokens, a generalized linear mixed-effects model was performed. The model selected included fixed effects for training difficulty level and by-subject random intercepts (the maximal model for this analysis). The model revealed a significant main effect of training difficulty ($\chi^2 = 102.98, p < 0.0001$), indicating higher accuracy on “easier” blocks consisting of larger intervals on the continuum.

Accuracy on the explicit perceptual fading training was comparable to the vowel tokens, despite participants only having a single day of training (see Table 1, Figure 4A), which was expected from previous pilot testing. A generalized linear mixed effects mixed-effects model with logit link function was fit, which included fixed effects of training difficulty level, stimulus type (Vowel vs. Sine), and their interaction, along with by-subject random slopes and intercepts for all fixed effects and their interactions. P values were estimated using a likelihood ratio test. The model output indicated yielded a significant main effect of block ($\chi^2 = 29.33, p < 0.0001$), indicates that participant’s accuracy decreased as training difficulty increased, regardless of stimulus type, as well as a main effect of stimulus type ($\chi^2 = 4.39, p = 0.04$), in that accuracy was higher for the Sine stimuli compared to the Vowel stimuli. The interaction between block and stimulus type was non-significant ($p = 0.07$).

Sine continuum categorization

Participants’ accuracy at identifying the endpoints of the Sine continuum was not as robust as the vowel continuum, but still reached at least 75% accuracy at each endpoint token (Figure 4B). This was confirmed by a generalized linear mixed-effects model where categorization responses in the Vowel (on the third training day) and Sine continua were compared. Fixed effects of continuum step, continuum type (Sine vs. Vowel), and their interactions, as well as random by-

DORSAL STREAM DECODING OF ARTICULABLE AND INARTICULABLE SOUNDS

subject slopes and intercepts for all fixed effects and interactions were entered into the model. P values were estimated using a likelihood ratio test. There was a significant effect of continuum step ($\chi^2 = 42.19, p < 0.0001$), but the effect of continuum type was non-significant ($p = 0.34$). However, there was a significant continuum step by continuum type interaction ($\chi^2 = 6.17, p = 0.01$). This interaction reflects reduced accuracy at the $/y/_{\text{Sine}}$ endpoint compared to the $/y/_{\text{Vowel}}$ endpoint.

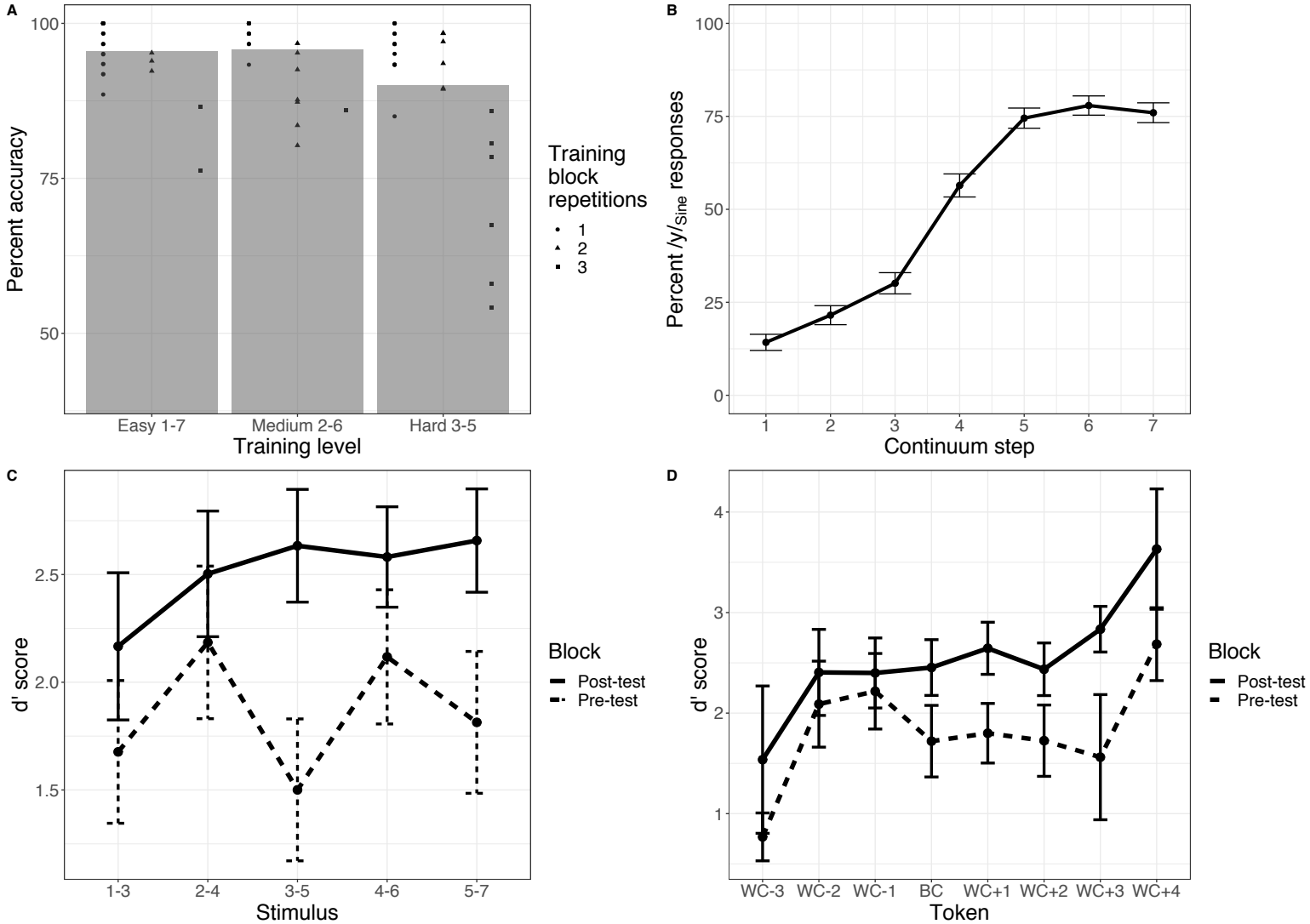


Figure 4. Behavioral data from the sine-wave training paradigm. A) Accuracy on the explicit perceptual fading training task for the sine-wave stimuli as a function of training level difficulty. Each point indicates an individual subject's performance, and the shape of the point indicates the number of times that participant repeated that block. B) Categorization data as a function of $/i/_{\text{Sine}}-/y/_{\text{Sine}}$ continuum step. Error bars indicate standard error. C) d' scores from the AX discrimination task for the sine-wave stimuli across each stimulus as a function of pre-test and post-test. Error bars indicate standard error. D) d' scores from the AX discrimination task for sine-wave stimuli with respect to the subject-specific determination of the "between-category" (BC) token. Error bars indicate standard error.

To assess potential differences in the mode of categorization between the two stimulus sets (i.e. categorical perception vs. more continuous perception), psychometric functions were fit to participant’s continuum categorization responses using the package *quickpsy* (Linares & López-Moliner, 2016) in R. The slope of the psychometric function was used as a tool to quantify how strongly categorical an individual’s perception, similar to the “categorical index” in Liebenthal et al. (2005, 2010). A t-test was performed on the slopes of the psychometric functions derived from the vowel and sine-wave categorization responses, which indicated that there was no significant differences in how categorically the two continua were perceived ($t(0.74)$, $p = 0.47$).

Sine AX discrimination task

Discrimination data was first separated into pre-test (the first discrimination task completed during that day’s training) and post-test (the final discrimination task following the continuum categorization task), and d' was again calculated for each of the resulting five “different” tokens for each subject (collapsing across 1 vs. 3 and 3 vs. 1, for instance). Again, token “3-5” was assumed to span the acoustic boundary and was treated as a “between-category” token, while the remaining four tokens were treated as “within-category” tokens (Figure 4C). A linear-mixed effects model was then performed on participant’s d' scores, with fixed effects of token type (between-category vs. within-category), block (pre-test vs. post-test), and their interaction, as well as by-subject random slopes and intercepts for all fixed effects and interactions.

The model revealed that there was no significant difference in d' between the “between-category” and “within-boundary” tokens ($p = 0.73$). However, there was a main effect of block, in which d' scores overall increased from pre-test to post-test ($F = 6.47$, $p = 0.02$). The interaction between token type and block was not significant ($p = 0.56$). Recoding the data to use subject-specific determinations of the “between-category” token did not alter the results (Figure 4D).

1.5.1 fMRI results

Imaging data from Sine and Vowel tokens were pooled in two analyses; a univariate approach to look for differences in activation magnitude, and a multivariate approach to investigate differences in activation patterns.

Table 2. *Results of ANOVA on fMRI data*

Area	Cluster Size (Voxels)	x	y	z	Maximum t Value
<i>Sine > Vowel</i>					
L STG, L RO	1807	-45	-11	6	7.85
R STG, R RO	1777	47	-9	6	9.55
L Cere. (Crus 2), L Cere. (Crus 1)	150	-15	-69	-34	3.90

STG = Superior Temporal Gyrus. RO = Rolandic Operculum. Cere = Cerebellum. Clusters corrected at the voxel level of $p < .025$, with 149 contiguous voxels and a corrected threshold of $p < .05$.

1.5.1.1 Univariate analysis

Contrasting functional activation for vowel tokens compared to sine-wave tokens (Figure 5, Table 2), three prominent clusters emerged, all showing more activation for sine-wave tokens compared to vowel tokens. Significant activation differences were found in a large right hemisphere cluster in STG extending into the Rolandic operculum, insula, temporal pole, and Heschl's gyrus, an analogous left hemisphere cluster in STG extending into Heschl's gyrus, Rolandic operculum, and temporal pole, and a smaller cluster in the left cerebellum.²

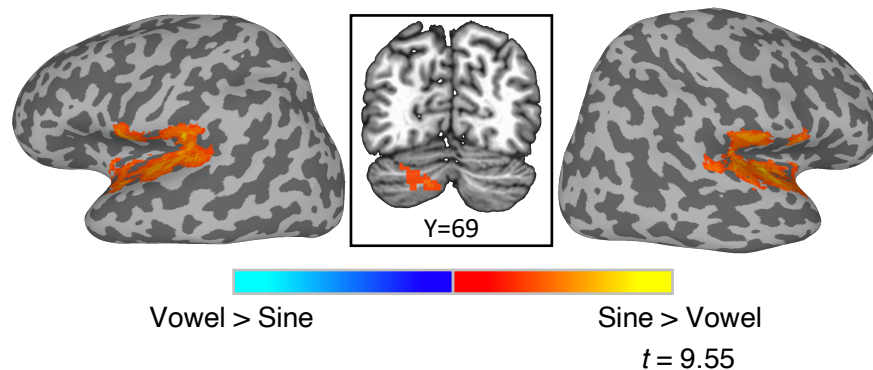


Figure 5. Regions that showed greater activation for sine-wave tokens than vowel tokens in the ANOVA. Clusters corrected at the voxel level of $p < .025$, with 149 contiguous voxels and a corrected threshold of $p < .05$.

² To investigate how individual differences in proficiency with the two continua may have impacted neural results, a linear-mixed effects model (with fixed effects of stimulus type and continuum step, and by-subject random intercepts) was performed on the functional data using AFNI's *3dLME*. Accuracy on the hardest level of difficulty for the explicit perceptual fading training for both the vowel tokens and sine-wave tokens on the final day of training was selected as a covariate. After controlling for participant's proficiency with the two continua, similar bilateral STG clusters emerged in which sine-wave tokens elicited greater activation than vowel tokens.

1.5.2.2 Multivariate analysis

Subject-level classification accuracy maps from the searchlight MVPA analysis were submitted to single sample t-tests against chance level (50%) to determine cortical regions that were able to discriminate category differences (e.g. all “A” tokens vs. all “B” tokens). For the decoding of the two vowel categories ($/i/_{\text{Vowel}}$ vs. $/y/_{\text{Vowel}}$), three significant clusters were found: (1) a cluster in right middle temporal gyrus extending into right superior temporal gyrus, (2) a cluster in the right inferior frontal gyrus (specifically in the Pars Triangularis and Pars Opercularis), and (3) a cluster in left middle temporal gyrus (see Table 3, Figure 6B). The same analysis for the sine-wave speech tokens, decoding $/i/_{\text{Sine}}$ vs. $/y/_{\text{Sine}}$ did not yield any regions that met the threshold for significance, but voxel-level decoding results from the searchlight analysis contributed to the Vowel decoding – Sine decoding comparison below.

Table 3. Results of t tests performed on MVPA classification data

Area	Cluster Size (Voxels)	x	y	z	Peak Accuracy
<i>$/i/_{\text{Vowel}}$ vs. $/y/_{\text{Vowel}}$ decoding</i>					
R MTG, R STG	200	47	-7	-12	51.64%
R IFG	181	49	19	30	51.66%
L MTG	159	-53	-43	2	51.47%
<i>$/i/_{\text{Sine}}$ vs. $/y/_{\text{Sine}}$ decoding</i>					
No significant clusters	-	-	-	-	-
<i>Vowel Decoding – Sine Decoding</i>					Maximum t Value
L Thalamus	422	-21	-17	6	3.04
L Insula, L TP, L RO, L IFG	404	-33	-5	20	2.94
L MTG	288	-47	-59	6	2.87
R SMA, R MCC, L SMA	227	9	-17	44	2.93
R Cere (VI) R Cere (IV-V)	191	15	-53	-22	2.97
L Cere (IV-V), Cere. Verm. (4/5)	186	-3	-57	-8	3.18
R HC, R Put.	171	27	-29	0	3.06
L Cere (VI), L Cere (Crus 1)	162	-23	-55	-26	2.93

MTG = Medial Temporal Gyrus. STG = Superior Temporal Gyrus. IFG = Inferior Frontal Gyrus. TP = Temporal Pole. RO = Rolandic Operculum. SMA = Supplementary Motor Area. MCC = Middle Cingulate Cortex. Cere = Cerebellum. HC = Hippocampus. Put = Putamen. Clusters corrected at the voxel level of $p < .025$, with 149 contiguous voxels yielding a corrected threshold of $p < .05$.

Next, we contrasted the sine-wave and vowel decoding maps to identify regions that differed significantly in decoding performance for the two stimulus sets. Subject-level classification accuracy maps from the sine-wave and vowel decoding analyses were submitted to a paired-samples t -test to identify regions that showed significantly different decoding performance for Vowel category differences than for Sine category differences. All such clusters showed superior decoding of Vowel contrasts, and included a cluster that extended from left insula into left temporal pole and left inferior frontal gyrus, as well as another cluster in left middle temporal gyrus (Table 3, Figure 6A).

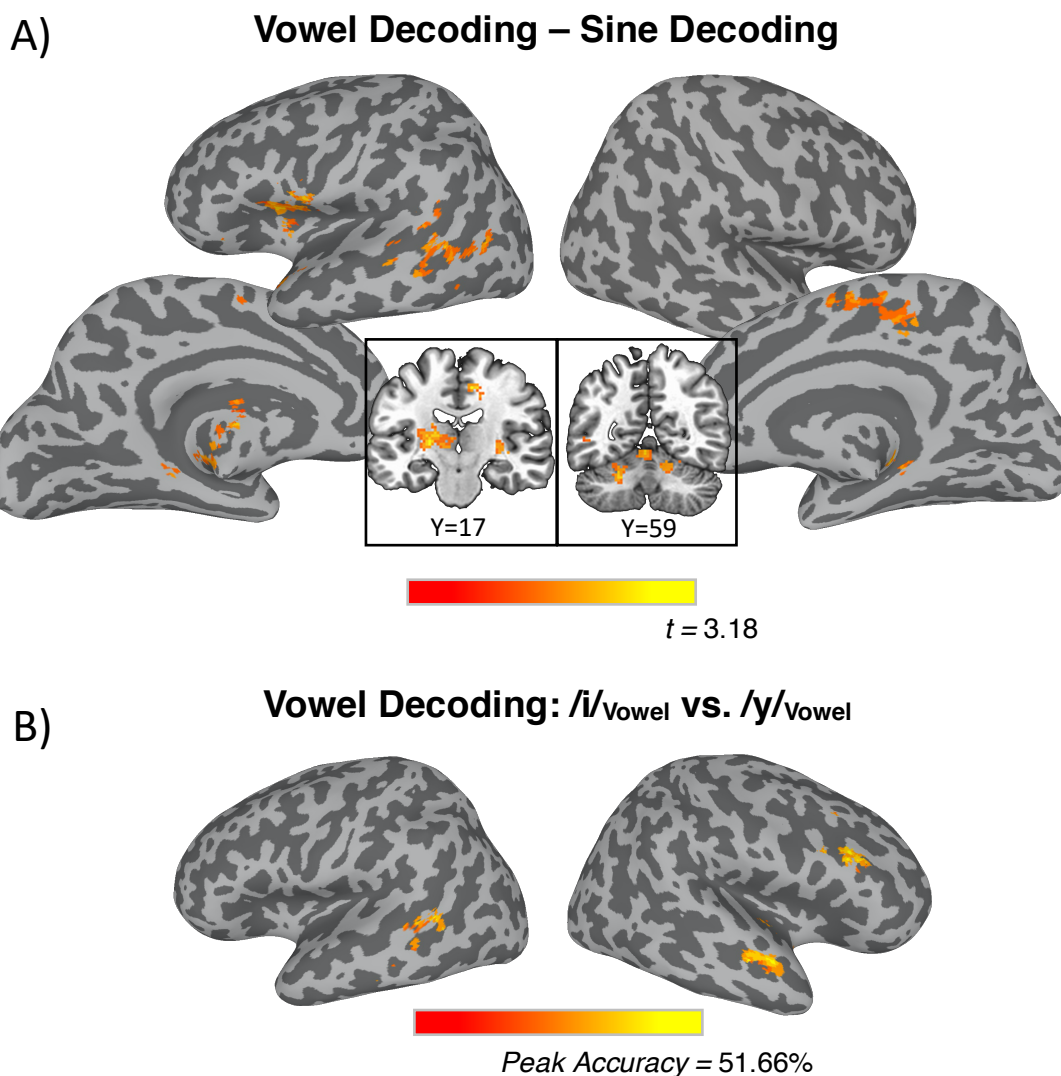


Figure 6. Results from the MVPA analyses. A) Output from the paired t test showing regions that classified Vowel categories significantly more accurately than Sine stimuli. Pop-out image displays cerebellar clusters and thalamus cluster not rendered in surface image. B) Regions that showed significant classification of the two Vowel categories. Clusters corrected at the voxel level of $p < 0.025$, with 149 contiguous voxels and a corrected threshold of $p < 0.05$.

Discussion

Behavioral Results

Over the course of several days, participants were trained on an unfamiliar non-native vowel contrast and its sine-wave analogue. On average, participants' ability to both identify and discriminate between the two categories in each continuum increased with training, and ultimately performance on the explicit perceptual fading training was not significantly different between the two continua. By the end of the third day of training, the two sounds from the vowel continuum showed a behavioral pattern that qualitatively resembles native-like perception (i.e. increased sensitivity across category boundaries and decreased sensitivity within category boundaries, Liberman, Harris, Hoffman, & Griffith, 1957). On the last day of training, d' values from the AX discrimination task for within-category tokens, (e.g., 1-3 or 5-7) were much lower than on the first day of training, whereas d' scores increased for the tokens most often containing participant's perceptual boundary (2-4 and 3-5). These results are congruent with previous studies of native English speakers' perception of the front-rounded vowel /y/, which show that listeners will initially assimilate /y/ onto the American English vowel /i/. Nonetheless, this contrast is ultimately learnable to a high level of proficiency (Levy & Strange, 2008; Levy, 2009).

Participants did reach similar levels of overall proficiency with the sine-wave continuum as intended (as measured by accuracy in the explicit perceptual fading training task), and results from the continuum categorization task indicate that there was no significant difference in our proxy for category structure (the slope of participant's categorization functions). Several studies of the perception of sine-wave speech continua have found that participants' responses were either random or largely continuous (Grunke & Pisoni, 1982; Johnson & Ralston, 1994, exp. 1; Desai et al., 2008), though a sine-wave speech version of a vowel continuum was perceived categorically regardless of whether the listeners interpreted them as speech or non-speech (Johnson & Ralston, 1994, exp. 2), which is likely more reflective of the results in the present study. The patterns observed in the sine-wave AX discrimination task are difficult to interpret in light of the continuum categorization results; there was no change in sensitivity for between-category or within-category tokens, indicating a lack of the acquired similarity and acquired distinctiveness that accompanies speech sound categories. However, this may simply be due to a

lack of exposure and could be refined over time, as there is little research into discrimination performance on a sine-wave speech contrast over several days of training.

fMRI Results

In general, greater activation for the sine-wave tokens in the univariate analysis points to the possibility that they were being processed less efficiently by a general auditory, and not speech-specific, mechanism. A broad scale contrast of areas where sine-wave tokens elicited greater activation than vowel tokens revealed bilateral clusters in STG, similar to the findings in Liebenthal et al. (2010), where non-speech stimuli showed greater activation than speech stimuli at post-test in STG. This could be due the fact that the sine-wave tokens were still more novel and participants had less of an opportunity to habituate to them. However, our results replicate Liebenthal et al. (2010), where participants were trained over the course of four sessions on their non-speech stimuli, suggesting that mere lack of exposure is not the only driving factor behind the sine-wave vs. vowel activation differences. Given the broad scale of dimensions that vary between the two stimulus sets, e.g. articulatory information or acoustic complexity, it is difficult to draw conclusions about the driving force of these neural differences using only univariate methods.

Regions identified in vowel decoding analysis are outside of dorsal stream

As discussed earlier, the dual stream model posits that the dorsal stream is recruited during the learning of speech sounds, where it serves as an auditory-motor integration mechanism. Evidence for this role has been difficult to ascertain given that many previous studies have used stimuli where only the inarticulable stimuli were unfamiliar (e.g. Liebenthal et al. 2005, 2010). To more conclusively answer this question, we trained participants on an unfamiliar vowel contrast, and used multivariate decoding analyses to investigate which brain regions could represent the differences between these sounds. Any region that can decode these newly-learned vowel categories could do so by virtue of access to (1) articulatory differences (lip rounding differences that listeners infer or extract from the auditory input), (2) abstract phonological categories (/i/ vs /y/), or (3) the acoustic differences between the two sounds (F3 is higher in /y/). We found that the right MTG and right STG were sensitive to vowel category information. Crucially these areas are not included in the dorsal stream nor implicated in speech-motor

processing, but *have* been identified in previous imaging studies of non-native phonetic learning (Callan et al., 2003; Wong, Perrachione, & Parrish, 2007). Additionally, another significant cluster was found in right IFG, which along with right MTG, has been implicated as playing a role in perceptual learning for speech, as Myers and Mesite (2014) found it to be sensitive to changes in representation of an /s/-/ʃ/ contrast in response to a talker-specific artificial accent. Right IFG has also been shown to be sensitive to nonlinguistic acoustic processing, like pitch (Wang, Sereno, Jongman, & Hirsch, 2003), as well as play a role in non-native phonetic learning (Myers & Swan, 2012). Thus, it is more likely that decoding sensitivity in these right hemisphere regions is based upon differential representations of the abstract categories of /i/_{Vowel} and /y/_{Vowel} and not the differences in articulation between them (or simply the acoustic differences). The only left hemisphere region that successfully decoded the two vowel categories was left MTG, and the cluster overlaps strongly with the phonological network described as part of the ventral-stream (Hickok & Poeppel, 2007). As such, our preferred interpretation of this pattern is that the left MTG likely represents phonological category differences between /i/ and /y/. The failure to find evidence for dorsal stream representation of different speech sounds during phonetic learning, when it is predicted by the dual stream model, suggests that articulatory information is either coded in non-speech motor areas (like right MTG and STG) along with phonological representations, is represented at a level that our multivariate analysis is not sensitive to, or is simply not recruited during this task.

Dorsal stream identified only when vowel decoding is contrasted against sine-wave decoding

It is possible the sensitivity to newly-learned vowel categories reflects acquisition of any new auditory categories, and is not speech-specific. In order to differentiate these possibilities, we compared classification results from the /i/_{Vowel} vs. /y/_{Vowel} and /i/_{Sine} vs. /y/_{Sine} decoding maps. The resulting statistical map indicates regions that better decoded the two different vowel categories than the two sine-wave categories, or put differently, regions that are sensitive specifically to auditory contrasts that differ in articulation. The critical comparison of interest is whether dorsal stream regions show discriminable patterns of activation *only* during the learning of articutable sounds (Vowel) but not non-articutable sounds (Sine), as would be predicted by the conception of the dorsal stream as an auditory-motor integration mechanism. Several dorsal stream regions emerged from this analysis; left IFG and left insula, bilateral supplementary motor areas, and a

left MTG extending into posterior STG (see Figure 6A) all showed superior decoding of vowel tokens compared to the sine-wave analogues.

These results are consistent with several TMS studies of the role of motor regions in speech perception, in which “artificial lesions” of speech motor regions (i.e., primary and pre-motor cortices) lead to changes in discriminating or identifying *native language* speech sounds, indicating a causal role of the articulatory regions during speech perception (Rogers, Möttönen, Boyles, & Watkins, 2014, Möttönen and Watkins, 2009, Krieger-Redwood, Gaskell, Lindsay, & Jefferies, 2013, Sato, Tremblay, & Gracco, 2009, Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007, Smalle, Rogers, & Möttönen, 2015). However, these studies have not necessarily addressed the dorsal stream as circuit though, instead focusing on one of the constituent regions. For instance, Krieger-Redwood et al., (2013) showed that stimulation of dorsal stream regions affected phonetic decisions, but not performance on a more naturalistic task where listeners had to match a word to a sample picture. Murakami, Kell, Restle, Ugawa, & Ziemann (2015) applied TMS simultaneously to left TPJ and left IFG (two of the three regions of the dorsal stream) and found decrements in phonological processing only in noisy conditions, which suggests that the dorsal stream may only be brought online during perception when stimulus identity is unclear. Following this logic, when listeners in our study needed to identify /y/, which overlaps perceptually with several native-language vowels and thus whose identity is less clear, the dorsal stream would be recruited. By the same token, it would likely not be recruited for the sine-wave speech stimuli, which do not share perceptual categories with any native-language sounds and thus whose identity is easily resolved.

The results from the paired analysis do provide support for the dual stream model’s conception of the dorsal stream as an auditory-motor integration mechanism, but we hesitate to conclusively accept this interpretation. As we will discuss in the next section, no brain regions significantly decoded sine-wave stimuli, which means that the paired analysis is displaying areas that have higher accuracy in the vowel decoding, but nevertheless do not reach significance in the vowel decoding alone (there was essentially no overlap between the map generated by the paired analysis and the map generated by the vowel decoding beyond left MTG). To that end, we believe the results from the vowel decoding, which do not involve any dorsal stream regions,

sufficiently address the original motivation of this study. Had both the vowel and sine-wave decodings yielded several significant, overlapping clusters, the paired analysis may have been more informative. However, as no dorsal stream regions were implicated in the vowel decoding alone, the comparison to an inarticulable analogue becomes less necessary. Based upon these results, future research should step back and more thoroughly examine if the dorsal stream is actually involved in phonetic learning at all.

Gradient neural representations of sine-wave stimuli may have impeded decoding

The sine-wave decoding analysis did not uncover any brain regions that reliably represented the two sine-wave categories. This is a bit of a puzzle given strong behavioral evidence that participants were able to distinguish the categories. One explanation for the failure to find neural sensitivity to sine-wave tokens appeals to the degree to which these stimuli showed “acquired equivalence” within the sound category. In speech processing, acoustic cues to speech sounds are initially encoded continuously at the neural level (Blumstein, Myers, & Rissman, 2005; Frye et al., 2007; Toscano, McMurray, Dennhardt, & Luck, 2009), then categorical structure is imposed on them quickly and neural responses begin to reflect phonological category membership early in processing (Toscano, Anderson, Fabiani, Gratton, & Garnsey, 2018). We speculate that by contrast, non-speech categories such as the sine-wave speech tokens used in the current study may continue to be represented in a graded fashion at the neural level. Because our analysis favored grouping of two more perceptually distinct sine-wave stimuli to reflect a single category (e.g., steps 1 and 3 for /i/_{Sine}), this could have created a more difficult classification problem for sine-wave tokens³. Submitting just the endpoints of the sine-wave continuum (step 1 & step 7) to the same decoding analysis yielded a significant cluster in right MFG. Notably, this analysis suffers from less power than that reported in the main body of the text, using only half of the tokens in the decoding analysis. This finding contrasts with a previous multivariate fMRI study of trained non-speech novel auditory categories that found that bilateral primary auditory cortex activation could successfully classify the two categories (Ley et al., 2012).

³ On the topic of classifier accuracy, observed accuracy at the group levels were numerically low, but statistically reliable. For the goals of this experiment, maximizing accuracy of the classifier is not of primary importance; significantly above-chance findings indicate that there is structured neural patterns in response to different stimuli, and using accuracy levels as a measure of the size of this effect is a faulty assumption. For a detailed explanation of the differences between MVPA for interpretation versus prediction, see Hebart and Baker (2018).

Subcortical regions implicated only in learning of speech sounds

Speech sound processing, especially during learning and adapting to speech sound variants, may not be limited to cortical regions. In the present data, better decoding for the vowel contrast compared to the sine-wave contrast was found in left thalamus. Previous work has observed that the thalamus is sensitive to human speech sounds: Dahane-Lambertz et al. (2005) found that the thalamus was generally more active for speech rather than sine-wave speech analogues in humans, while Krauss et al. (1994) found that the guinea pig thalamus is sensitive to complex spectral differences between human speech sounds even when animals were not exposed to any kind of training on these sounds. However, more relevant to this goal of this study is the relationship between the thalamus and articulatory information; neuropsychological investigations have found that damage to the thalamus often yields difficulties with the articulation of speech sounds (Canter & van Lancker, 1986; Jonas, 1982; Wallesch et al., 1983), and our results suggest that during the learning of new speech sounds, the thalamus may be representing the articulatory codes that will later be used for production, similar to the role of the dorsal stream in the dual stream model.

More broadly, there has been increasing interest in the contribution of subcortical brain structures in experience-dependent plasticity in the auditory system (Chandrasekaran, Skoe, & Kraus, 2014), and it is suggested that the cerebellum is involved in adaptation to alterations in speech through its functional connectivity to cortical language areas (Guediche, Holt, Laurent, Lim, & Fiez, 2015). In the present study, the significant right cerebellar clusters may reflect the engagement of this language plasticity network (similar to Guediche et al., 2015) as a result of the nascent formation of a speech sound category. Language related cerebellar function is heavily right lateralized, while left cerebellum, especially lobule VI and Crus. 1, are implicated as having a role in executive functioning. Left cerebellar engagement in this study could reflect a decision-making process about category membership for the vowel contrast (for a review, see Stoodley & Schmahmann, 2009).

Conclusion

In sum, the MVPA results from the present experiment provide support for the interpretation that dorsal stream regions are recruited during the learning of articable sounds only. While we did find evidence for dorsal stream recruitment when looking for regions that could preferentially discriminate category membership for articable contrasts (our vowel contrast) rather than inarticable contrasts (our sine-wave contrast), these regions did not appear when examining decoding accuracy for $/i/_{\text{Vowel}}$ vs. $/y/_{\text{Vowel}}$ alone. Instead, a series of regions outside of the dorsal stream previously implicated in non-native phonetic learning could successfully classify the two vowel categories. Future work will need to address the interplay between recruitment of the dorsal stream in the initial stages of phonetic learning and the contribution of right hemisphere cortical regions.

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